I wish to thank Dr. H. A. Wahl, Pennsylvania State University, for his advise and encouragement. Dr. J. R. Reeder and Charlotte G. Reeder provided many constructive comments on the manuscript. The expert field assistance of Robert C. Gardner is acknowledged. The drawings were executed by Barry L. Siler. This study was supported by NSF Grant GB-29193X.

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ECOLOGY OF THE SAGUARO (CARNEGIEA GIGANTEA): PHENOLOGY AND ESTABLISHMENT IN MARGINAL POPULATIONS

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The saguaro, *Carnegiea gigantea* (Engelm.) Britt. & Rose (Cactaceae), has been at the center of much scientific interest since Shreve (1910) reported its failure to reproduce in some localities. Additional observations that supported Shreve's conclusion (Gill, 1942; Gill and Lightle, 1946; Hastings, 1961; Alcorn and May, 1962; Niering et al., 1963; Alcorn, 1966) led to a number of studies aimed at defining the cause of the saguaro's decline (Shreve, 1911; Lightle et al., 1942; Alcorn and Kurtz, 1959; McGregor et al., 1962; Hastings and Turner, 1965;

Turner et al., 1966; Steenbergh and Lowe, 1969; Turner et al., 1969). Since saguaro population declines had been noted in many different environments, climate was suggested as affecting either germination or seedling survival, or both. It was the aim of this study to investigate the interaction of climate and saguaro survival in marginal populations and in so doing to identify the factors limiting the saguaro's geographical distribution.

Study Sites

Available data suggest that the most significant climatic factors affecting saguaro germination and establishment (seedling survival) are temperature and moisture. Since it is these climatic factors that apparently limit marginal saguaro populations in the North (temperature) and in the West (moisture), investigations in these areas may provide insight as to which of these climatic factors is more important in influencing saguaro germination and survival and/or limiting extension of the saguaro's range. Consequently a study site was established in each of two marginal populations. An additional study site, located more centrally within the range of the saguaro, was also established to provide a basis of comparison.

Site 1, the "control", is at the junction of U.S. Highway 93 and the Santa Maria River (Yavapai Co.) about 68 km north of Wickenburg, Arizona. This site, with an elevation of 1136 meters, was judged to be generally representative of saguaro populations (about 50 per hectare). Other dominant perennials occurring with the saguaro are *Cercidium microphyllum, Larrea divaricata, Acacia greggii,* and *Prosopis juliflora* (listed in order of abundance).

Site 2 is in the southern portion of the Haulapai Mountains (Mohave Co.) on Alamo Road 45 km southwest of Yucca, Arizona at an elevation of 595 meters. This area supports one of the northernmost populations of saguaros with the majority (about 37 per hectare) found on south-facing slopes. The study area supports the greatest numbers of species of both succulents and non-succulents of the sites investigated. Notable species present, in order of abundance, are *Opuntia bigelovii, Ambrosia dumosa, Opuntia acanthocarpa, Cercidium microphyllum, Larrea divaricata, Hymenoclea salsola, Fouquieria splendens,* and *Yucca brevifolia.*

Study Site 3 is in the Whipple Mountains (San Bernardino Co.) near the eastern border of California and runs along the Metropolitan Water District's access road west of Parker Dam. This site supports the most substantial population of saguaros found in California (ca 120 individuals) and is located on the western border of the saguaro's geographical range. Because of low saguaro density the study site is very large (about ten square km) and the elevation ranges from 107 to 366 meters. The density of saguaros is about four per hectare in the eastern part of the study site, where plants are limited to north-facing slopes; however, near the junction of Copper Basin Reservoir access road a very substan-

tial stand of saguaros (about 12 per hectare) occupies all the slopes of a circular range of peaks, with the greatest density on the southeast-facing slopes. The percent ground cover and densities of all species were lowest in this study area when compared with Sites 1 and 2. Dominant perennials in this area, other than the saguaro, are *Larrea divaricata, Hymenoclea salsola, Opuntia bigelovii,* and *Encelia farinosa* (in order of abundance). *Cercidium microphyllum,* also a dominant, occurs predominantly in the washes.

Materials and Methods

Shreve (1910) and later Hastings and Alcorn (1961) measured the rate of growth of selected individuals of the saguaro and determined a relationship between height and age. This relationship was used in the present study to estimate age and germination dates of sampled individuals. On the basis of the number of individuals surviving within each height class (set at 61 cm intervals), saguaro establishment (i.e., germination and seedling survival) was compared in the three study areas. Then by correlating saguaro establishment periods (i.e., the number of saguaros that germinated and survived to present during the time interval corresponding to the 61 cm height increment) with available weather records, climatological requirements for establishment in each study area were estimated.

Saguaro heights were determined on two different dates at each study site. Data were first collected on December 28, 1971, for Sites 1 and 2, and on January 12, 1972, for Site 3. Individual heights were estimated with the use of a fixed 6-foot standard placed beside the cactus. Heights of additional individuals were determined on April 28 and 29, 1972, using a graduated telescoping aluminum pole, capable of expanding to 7.5 m. Selection of individuals for height measurements was by random selection of a sampling area within the study site and then quota sampling within that area.

Because shade, which may be provided by closely associated plants ("nurse-plant") or rocks ("nurse-rocks"), has been shown to be a basic requirement for seedling survival (Turner et al., 1966), the species of "nurse-plant" or the indication of a "nurse-rock", if present, was noted at the time of height determination. In a few cases where only "nurse-plant" remains were found, no attempt was made at the plant's identification, but the association was recorded. Vigor of the saguaros sampled was estimated on a scale of 0 (dead) to 3 (healthy).

To provide phenological comparison between study sites, reproductive activity was recorded. Selected individuals were tagged and the numbers of flower buds and open flowers were counted. Twenty-five saguaros were sampled in each study area on April 28 and 29, 1972, and on May 27 and 28, 1972, the numbers of flowers maturing into fruit on these individuals were recorded. The selection of individuals was also done by random selection of a sampling area within the study site and by quota sampling of adjacent individuals of reproductive age.

Results and Discussion

Height class frequencies for the three study sites are shown in Figure 1. Comparison of the means of the estimated heights and of the measured heights for each sample showed agreement at the 95 percent confidence level; therefore all height determination data are included in the figure and calculations. A close similarity between Sites 1 and 2 is most notable when comparing height classes and establishment patterns. Approximately 37 percent of the individuals sampled became established in both Sites 1 and 2 between 1916 and 1936, with maximum establishment during the period 1924–1930 (13 percent and 14 percent respectively). However, in Site 3 only 5 percent of the individuals sampled had become established between 1924–1930 and a total of only 17 percent between 1916 and 1936. The Site 3 establishment pattern also differs during the period 1908–1915 when 20 percent of the sampled individuals became established; Sites 1 and 2 show only 4 percent and 3 percent, respectively. The close similarity of establishment patterns of Sites 1 and 2, and the more or less opposite relationship for Site 3 could suggest error in applying growth rate data from saguaros that were measured in the Saguaro National Monument (i.e., by Hastings and Alcorn, 1961) to those individuals found near Parker Dam (Site 3). Or, this relationship may suggest that conditions for germination and establishment are very different during the same periods of time in areas near Site 3 than those near Site 1 and Site 2. But, similar establishment periods can also be noted for all three study sites (1900–1907, 1916–1923, 1927–1940). With both contrasting and similar establishment patterns during the

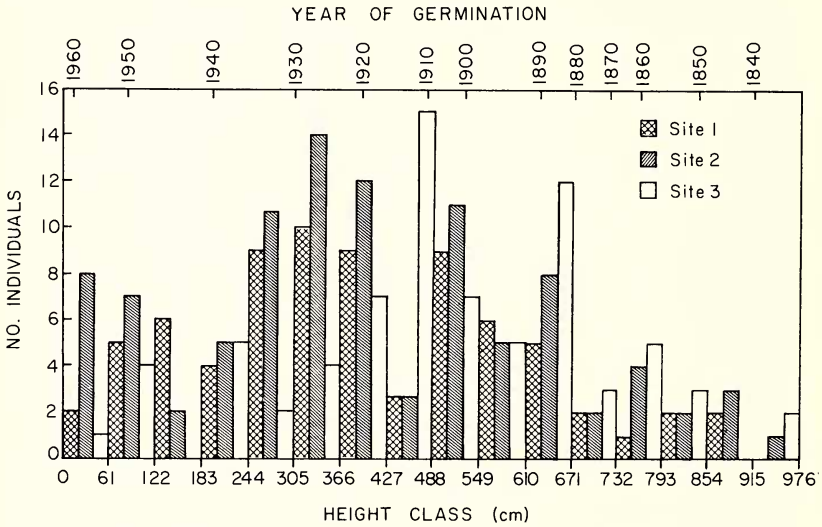

Fig. 1: Height-age distribution of saguaros in Sites 1, 2, and 3.

same periods for the three study areas it is impossible to resolve whether these establishment patterns are due to misapplication of growth rate data or to variations in germinating and survival conditions.

Shreve (1910) and later Hastings (1961) presented similar height and frequency studies for populations sampled in areas near Phoenix and Tucson, Arizona. They described how the slope of the height vs. frequency curve for a population gives an indication of the dynamic state of that population (i.e., whether it is increasing, stable, or declining). Applying this analysis to the populations included in this study, all study sites suggest declining populations. An exception may be Site 2, which indicates recent (1940–present) high establishment and low mortality (3 percent).

The majority of individuals in each study site were included in the healthiest vigor category (81 percent in Site 1, 89 percent in Site 2, 78 percent in Site 3) suggesting that most of the individuals have the capacity to reproduce (ability to produce flowers, fruits, and seeds). However, the phenological data presented in Table 1 indicate that a very low percentage of individuals actually did reproduce in 1972. At best only 32 percent (Site 1) of the individuals of reproductive age were observed in flower in 1972 and this percentage is below what would be found near Tucson, Arizona (R. Hastings, personal communication). In addition to the percentage of individuals in flower, the height and the range of height of flowering individuals also varied between study sites. The range of heights (and therefore age) of flowering plants was similar for Sites 1 and 2; however, in Site 3 no individuals less than 488 cm (60 years) were found in flower. Alcorn (1961) stated that saguaros begin to flower between the ages of 40 and 50 years (300 cm to 370 cm tall), and the individuals sampled in Sites 1 and 2 substantiate this.

Flowering individuals in Site 1 appeared to be uniformly distributed but in both Sites 2 and 3 there were distinct locations where flowering occurred. In Site 2 flowering individuals occurred only in washes and on higher slopes, and in Site 3 all the individuals found with flower buds

Table 1: Summary of Reproductive Activity of Tagged Saguaros

Parameter	SITE 1	SITE 2	SITE 3
Individuals with flower buds	32%	24%	8%
Range of heights (cm) of individuals with flower buds (Ave.)	335–793 (655)	366–823 (710)	488–640 (723)
Fruit set based on the percent of flowers	90%*	85%*	10%

* Flowers buds still maturing on date of sampling.

were located in washes. These location criteria and the indication that Site 3 is the most arid of the three sites (figs. 2, 3, and 4) suggest that flowering is influenced by moisture.

The percent of flowers developing into fruit was highest for Site 1 (90 percent), but the percent of flowers in various stages of fruit maturation in Site 3 was considerably lower (10 percent). Although nighttime pollinator analysis was not included in this study, the abundance of daytime pollinators (hummingbirds, bees, wasps, and beetles) and the fact that at least a low percent of flowers matured into fruits suggest that the poor fruit set is not the result of a lack of pollinators here—even though those noted are not the saguaro's most commonly identified pollinating agents (McGregor et al., 1959, 1962; Alcorn et al., 1959, 1961). Based on the number of individuals with flower buds and the percentage of fruit set, the establishment potential is less in the two marginal populations of saguaros than that found in the more central population. Declines in these populations may then be partially explained on the basis of low reproductive potential. However, because of the critical effects of temperature and moisture on seed germination and seedling survival (Kurtz, 1960), climatological influences on saguaro establishment must also play an important role in an explanation for population declines.

After germination an important factor for seedling survival is the amount of summer (July and August) precipitation, for it is during this time that the saguaro is most efficient in taking up water (Hastings, 1961). An additional barrier to seedling survival is the intensity of the dry, hot periods (May and June) preceding summer rainfall (Turner et

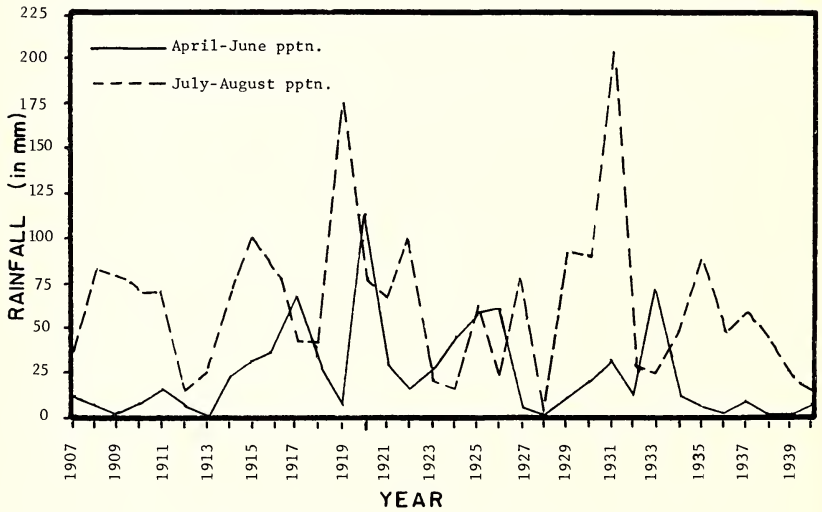

Fig. 2: Rainfall 1907 – 1940 for Site 1.

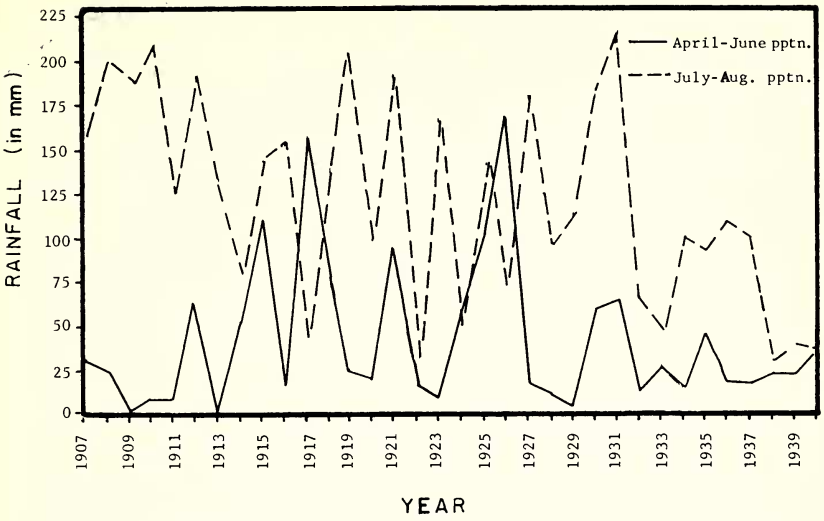

Fig. 3: Rainfall 1907 – 1940 for Site 2.

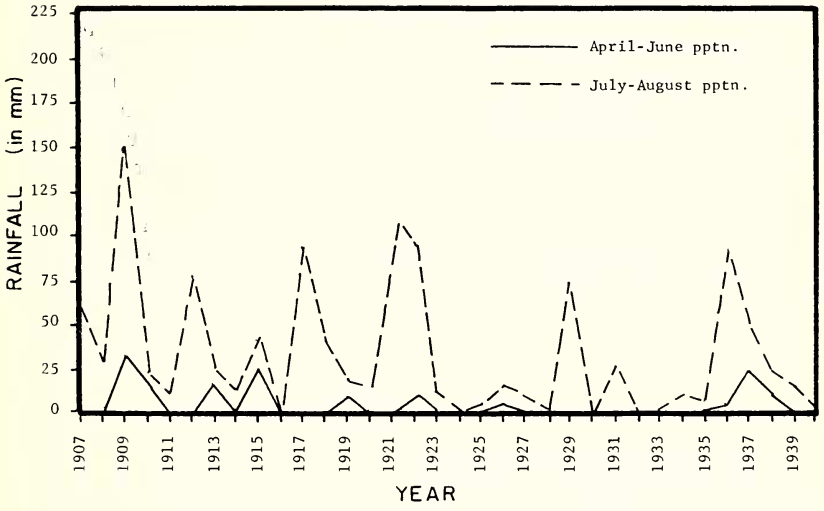

Fig. 4: Rainfall 1907 – 1940 for Site 3.

al., 1966). Climatic data from nearby weather stations (U.S. Weather Bureau, Climatic Summary of the U.S., 1893–1930, 1931–1952, 1951–1960; U.S. Weather Bureau, Climatological Data: Arizona, 1961–1965; U.S. Department of Commerce, Climatic Summary of the U.S. Suppl. for 1951–1960; U.S. Department of Commerce, Climatological Data: Arizona 1961–1965, 1966–1970; Headgate Rock Dam Weather Station

Records, 1953–1967) show that for Site 1 during the period 1907–1940 April–June and July–August precipitation correlates very closely with the number of saguaros established (fig. 2). The correlation supports the contention that there are particular precipitation requirements for both these periods and further suggests that without some minimal amount of precipitation during April, May, and June, regardless of the amount received during July and August, there would be very little or no establishment of saguaros. However, when April–June precipitation is sufficient to prevent dehydration of saguaro seedlings, the degree of establishment is proportional to the amount of precipitation received during the period from April to August. Thus the greatest establishment occurred when a year of high July–August precipitation was followed by a year with high April–June precipitation (e.g., 1916–1917 and 1925–1926, fig. 2). Precipitation data for the same period (1907–1940) are presented in Figure 3 for Site 2 and support this contention. The April–June precipitation requirement is more apparent for Site 2 for the figure shows significant establishment during a period of increasing April–June precipitation (1920–1926), which would allow for the survival of seedlings germinated over the entire six years. However, other factors (rodent populations, for instance) are also influenced by temperature and precipitation and may also be important to the observed patterns. The April–June precipitation requirement is not as definitive for Site 3, although the amount of July–August precipitation is again related to the degree of establishment (fig. 4). Site 3 experiences temperatures on an average of 2°C higher during the winter months and consequently some winter precipitation may be available to young seedlings for restoration of lost water.

Site 3 also differs from the other two study sites in having the highest percentage of individuals (86 percent) associated with "nurse-plants", even though potential "nurse-plant" density is the lowest (maximum of 75 plants per hectare). In Site 1 where "nurse-plant" density is high (10 times that of Site 3), 74 percent of the individuals were associated with a "nurse-plant" while in Site 2 with the highest density of potential "nurse-plants" only 10 percent of the saguaros were associated with "nurse-plants". Although the highest percentage of saguaros associated with "nurse-rocks" (15 percent) was in Site 2, Site 3 still had the greatest number of individuals (90 percent) associated with shade producing objects. Perhaps the explanation for the establishment of individuals in Site 3 during drier May–June periods is related to the protection offered by the shade of either "nurse-plants" or "nurse-rocks". Lowe and Hinds (1971) showed that radiation temperature is up to 25°C higher in the open than under a paloverde (*Cercidium* sp.) Thus a saguaro seedling growing under a paloverde might be subjected to less dehydration stress during the May and June hot, dry period than a seedling growing out in the open. All of the individuals with "nurse-plants" in Site 3 were associated with paloverdes and not with other, perhaps less protective, "nurse-

plants" found in the other study areas. Further analysis at Site 3 showed that individuals without a "nurse-plant" fell into distinct height categories (i.e., at 183 cm four out of five individuals were not associated with a "nurse-plant") and that the corresponding germination dates show the April–June period to be considerably wetter (four times) than periods when only saguaros with "nurse-plants" survived.

Conclusion

Data included in this study clearly support Shreve's conclusion that in many environments saguaro reproduction does not meet replacement requirements necessary to maintain stable populations. One explanation for the population declines may be low reproductive potentials such as those found for 1972 in each study site included in this investigation.

The climatic criteria for germination and establishment have been shown to be strict enough that only exceptional years of high summer and spring rainfall result in significant saguaro establishment. In addition, with climatic trends in opposition to establishment criteria for the saguaro, declines in some marginal populations (as indicated in this study) are to be expected. Populations in the more northern portions of the saguaro's range may however, increase in size and number in future years because of the general climatic trend of increasing temperatures. For the western boundary range expansion does not seem likely, for weather data indicate that the saguaro establishment requirements are only rarely met in California deserts. Indeed, population declines and range reduction in California are more likely to occur in the future.

Acknowledgement

I express appreciation to the Department of Biology, University of California, Riverside, for support and the use of its facilities during the course of this study. Special thanks is given to Dr. Frank C. Vasek for valuable suggestions, comments, and criticism.

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CALIFORNIA SPECIES OF CORDYCEPS PARASITIC UPON ELAPHOMYCES

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During the past several years *Cordyceps capitata,* a pyrenomycetous parasite of *Elaphomyces,* has been found in the coastal forest of California from Sonoma County northward to Del Norte County and often abundantly so in Mendocino and Humboldt counties. Recently one of